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ECOLOGICAL RELATIONS OF PLANTS IN SOUTHEASTERN MISSOURI

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The state of Missouri can be divided physiographically into three distinct regions: (1) the prairie region or glacial plain in the northwest and a prairie region in the middle west; (2) the Ozark region toward the south, southwest, and partly southeast; and (3) the lowlands in the southeastern corner.

The writer has made his botanical observations in the southeastern part of the state; to which belong a large part of the Ozark uplift and the lowlands in the extreme southeast. Counties which were mainly studied are Madison, Iron, Reynolds, Wayne, St. Francois, Bollinger, Carter, Ripley, Butler, where an important part of the Ozark Mountains is located, and Butler, Stoddard, Scott, Mississippi, New Madrid, Dunklin, and Pemiscot, where most of the lowlands are found.

The plant growth of this section of the state has hardly been studied; therefore no data of other investigators could be examined with the exception of those who explored other parts of Missouri such as Mackenzie (4), Daniels (2), and Hus (3). Only Bush (1) made some collections in this part of the state, and published a list of specimens found.

The author is much indebted for the kind help he received from Mr. C. A. Gierth of Poplar Bluff, Mo.

Excursions were made by the writer in 1918 throughout the entire spring and summer; the various plant associations in relation to their environment were studied, with the exception of those which are the result of the activities of mankind, such as the plant growth along canals, railroads, on cultivated farms, and so on.

The Ozark region, as it appears in the counties above named and in others not mentioned here, is composed not of an arrangement of mountain chains but of short ridges and rounded peaks with numerous valleys. The highest peaks in this part are to be found in Iron County, attaining a height of 540 meters; in this county occur the greatest variations in altitude of the entire Ozark Mountains; in St. Francois County the highest elevation is about 330 meters; whereas the highest hill in Butler County is about 200 meters above sea level.

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Geologically the Ozarks are complex; crystalline rocks are to be found in the southeastern part of the state, namely in the St. Francois Mountains, which are considered oldest. Further, several beds of limestone and sandstone are to be met. The various systems are either Carboniferous, Devonian, Silurian, Ordovician, Cambro-Ordovician, or Cambrian.

Erosion has played an important part in the topography of the country; therefore soil types are of various kinds and to a considerable extent derived from the various rocks in their respective environment. The physical properties of these soils greatly influence the development and the differentiation of the flora; they are grey to reddish-brown in color, contain but little organic matter, often stones are present, and rock outcrops are very common. Level areas are the least stony as a rule. The reddish-brown soils are usually derived from cherty limestones of the lower Carboniferous group, the grey soils derived from the Cambro-Ordovician group being silicious limestones. The oxidation of iron gave to the soil a reddish-brown color, which is absent in grey soils of the cherty limestones. The character of the soil varies from a stony to a silt loam.

Many streams and creeks traverse the country and are the cause of constant erosion, giving to a large extent the present aspect of the topography of the Ozarks. Outside the rainy periods they are harmless little streams, often entirely dry during the largest part of the summer; after heavy rains, or sometimes after sudden melting of a heavy snowfall, they grow to wide streams, overflowing the surrounding country and denuding areas of a part of the soil and vegetation, and often giving a different aspect to the environment.

The climate of the southeastern part of Missouri is characterized by hot summers and mild winters. The temperature data which the writer was able to obtain are given in table I.

TABLE I. *Temperatures in Southeastern Missouri*

Month	Mean	Maximum	Minimum
	° C.	° C.	° C.
January.....	— 1.11	+ 3.33	— 5
February.....	+ 0.55	5.55	— 3.33
March.....	8.89	13.30	+ 2.78
April.....	15	20.55	10.55
May.....	18.89	25	13.89
June.....	25	31.10	20.55
July.....	31.67	40.55	24.44
August.....	31.11	38.89	23.30
September.....	24.44	31.67	20
October.....	16.10	22.22	11.10
November.....	8.89	16.11	3.85
December.....	5	10	— 0.55

In the higher portions of the mountain ridges and peaks the temperature is lower. Considerable cold spells are of short duration; in some winters

there is no snowfall. The average snowfall amounts to 275 mm. in the southeast, as compared with 600 mm. in the northwestern part of the state.

The atmosphere is very humid and depressing. The rainfall in southeastern Missouri is higher than that in any other part of the state. Although no exact data could be obtained, the following were derived from sources of the United States Weather Bureau: 800 to 950 mm. in parts of northern Missouri, 950 to 1,100 mm. in the middle section, 1,100 to 1,500 mm. in the southeast being the mean annual rainfall over 21 years. During the summer rainless periods may occur of 2 to 6 weeks' duration; whereas sudden, heavy rainfalls accompanied by thunderstorms may occur at any time during the summer; these rains swell the rivers suddenly and cause them to overflow the surrounding country, especially the lowlands.

The mean growing period of the vegetation lasts from March to October.

Plant associations are very much diversified on account of their localities, such as small river valleys, ravines, barrens, mountain summits, rock outcrops, and small prairies; each one has its own plant societies. Frequently species are encountered belonging to southern states which are not to be found in the northern or middle part of the state.

The forests of the Ozark hills are a predominant feature, being entirely different in composition from those of the lowlands. The soil of these hills is poor in organic matter as far as the slopes are concerned; the reddish-brown or grey soil, composed of very fine particles, is everywhere visible; when wet it is very sticky, when dry it is baked and very hard. Various oak species are here in the majority; although in a certain area one species of oak may be more frequently observed than in any other part of the hills. Toward the southern portion, e.g., in Butler County, *Quercus marilandica* Muench. forms a considerable part of the forest growth; in richer uplands *Quercus imbricaria* Michx. is often present; other species which are never absent are *Q. stellata* Wang.; *Q. falcata* Michx.; *Q. macrocarpa* Michx.; *Q. alba* L.; *Q. rubra* L.; hybrids of *Q. alba* × *Q. macrocarpa* and of *Q. rubra* × *Q. falcata* are also sometimes observed. The heaviest trees are always referable to *Q. alba*, *Q. macrocarpa*, and *Q. rubra*.

Other genera of trees met with in such dry hills are, in the first place, several hickories, especially *Carya glabra* (Mill.) Spach, *C. ovata* (Mill.) K. Koch; where the soil is more fertile big trees of *C. alba* (L.) K. Koch also become common. Further, *Diospyros virginiana* L., *Liquidambar styraciflua* L., *Sassafras officinale* Nees & Eberm., and *Nyssa sylvatica* Marsh. occur on such sterile soils; they become, however, far more common when the soil is fertile. Of smaller kinds of trees one notices especially in the spring before the leaves are unfolded the early flowering *Cercis canadensis* L., although it is as abundant in the rich bottom lands and ravines; at this time of the year the trees are covered with the beautiful pink-colored flowers; *Cornus florida* L. also grows in practically the same localities. On the other hand, *Ulmus alata* Michx., a species with conspicuously winged

twigs, belongs decidedly to the dry, sterile uplands of the above mentioned counties.

The composition of these forests as far as the various species of trees are concerned is expressed in table 2, the result of surveying typical hills densely covered by woods in a few counties.

TABLE 2

Name of Tree	A Forest in Western Butler County %	A Forest in Middle Iron County %	A Forest in Middle Wayne County %	A Forest in Southern Madison County %	Diameter of Thickest Tree Observed (dm.)
<i>Quercus marilandica</i> Muench.	25	6	15	—	3
“ <i>imbricaria</i> Michx.	0.3	20	—	—	8
“ <i>alba</i> L.	10	2	—	1	9
“ <i>rubra</i> L.	8	4	6	—	8
“ <i>macrocarpa</i> Michx.	23	10	10	30	12
“ <i>falcata</i> Michx.	14	15	—	12	6
<i>Carya glabra</i> (Mill.) Spach.	11	6	4	12	5
“ <i>ovata</i> (Mill.) Koch.	—	—	2	8	6
“ <i>alba</i> (L.) Koch.	—	4	6	—	6
<i>Juglans nigra</i> L.	—	—	2	—	9
“ <i>cinerea</i> L.	—	3	6	8	6
<i>Ulmus alata</i> Michx.	5	2	8	2	4
<i>Sassafras officinale</i> Nees & Eberm.	—	4	15	16	8
<i>Diospyros virginiana</i> L.	2	15	12	6	3
<i>Liquidambar styraciflua</i> L.	1	8	11	—	7
<i>Fraxinus americana</i> L.	0.7	1	—	—	7
<i>Nyssa sylvatica</i> Marsh.	some	—	—	2	8
<i>Cornus florida</i> L.	some	some	2	1	1½
<i>Cercis canadensis</i> L.	some	some	1	2	1

Of all these species *Quercus marilandica* is the most typically xerophytic species and especially adapted to dry barrens; where the hills are becoming fertile, as toward the base of the hill near a stream, this oak species disappears completely.

The shrub vegetation is not always heavily developed between the high trees, but is common toward the edge of the woods. Here are frequently found very extensive thickets of *Symphoricarpos orbiculatus* Moench covering several acres in extent, often forming a pure association where nothing else is found until the forests are entered, where the shrubs become gradually less abundant. Other species of shrubs and small trees which may grow either in pure stands or in a mixed growth are *Rhus typhina* L., *R. canadensis* Marsh., *Ribes gracile* Michx.; whole patches are covered by *Ceanothus americanus* L. and *Rosa* species, especially *R. blanda* Ait. and *R. pratincola* Greene, whereas in other areas *R. humulis* Marsh. is prevalent. In various hills of the above described type the slopes are entirely covered by *Vaccinium melanocarpum* Mohr extending into the *Quercus* facies, although in the latter places they do not grow so densely; they are especially common in the hills of the western portion of Butler County and in Wayne County;

although they occur also in other parts. In the southwestern part of Butler County and in the neighborhood of Poplar Bluff in the same county, several individuals were found of *Vaccinium arboreum* Marsh., of which the highest plant attained a height of $3\frac{1}{2}$ meters; the highest ones I met in this region grew in a scattered wood especially where *Quercus marilandica*, *Q. macrocarpa*, and *Carya ovata* were predominating trees in a sandy loam.

In spring the woods are covered with several early flowering plants, being to a large extent bulb- or rootstock-bearing species; whole areas form a dense association of *Podophyllum peltatum* L. where hardly anything else is able to find a place. Along other parts of such woods there are, either scattered or in small patches, *Anemonella thalictroides* (L.) Spach, *Viola pedata* L., *Oxalis violacea* L., and *Hypoxis hirsuta* (L.) Coville. These species are common where trees are less dense or in open parts of the woods, places which are very exposed to drought; but the rootstocks and bulbs of these species are well protected. The thick roots of *Anemonella*, containing reserve food, are surrounded by a tissue of cork; whereas the bulbs of *Oxalis* and *Hypoxis* are protected by a fibrous mass consisting of the remains of scales. Where the soil contains more moisture and humus, interesting growths of *Claytonia virginica* L., *Delphinium tricornes* Michx., and *Viola palmata* L. are to be noticed. The undergrowth of these woods and thickets is later, in the early summer, succeeded in the first place by large areas of *Potentilla canadensis* L. which are especially a feature of situations having a rather sandy subsoil. Where this species is not present the surface is practically everywhere covered by *Houstonia coerulea* L. which flowers until midsummer. Elsewhere, however, plenty of space is given to other species, where all those mentioned with the exception of few *Podophyllums* and *Potentilla* are growing; to which may be further added *Krigia dandelion* (L.) Nutt., *Fragaria virginiana* Duchesne, *Geum canadense* Jacq., and *Erigeron vernus* (L.) T. & G. With the exception of *Fragaria* these species practically never cover considerable areas, and therefore one cannot speak of a certain association. When woods are becoming somewhat exposed, such species as *Monarda bradburiana* Beck, *Silene virginica* L., *Sisyrinchium campestre* Bicknell, and considerable areas of *Antennaria plantaginifolia* (L.) Rich. abound.

Later in the year the early flowering species gradually disappear. *Houstonia* is to a large extent replaced by *Stylosanthes biflora* (L.) B.S.P., in other sections by *Lechea minor* L. or *Cunila mariana* L. Pure stands of each of the latter may cover one hill after the other. At this time of the year (from July to September) long rainless intervals often have much influence on the vegetation of these hills, for which the above named species are well adapted. On very exposed slopes only very drought-resistant species are to be noticed, among which *Euphorbia maculata* L., *Agave virginica* L., *Croton capitatus* Michx., and *C. monanthogynus* Michx. are commonest. Where plant growth is to a certain extent protected by the shade of only a

few big trees or by slopes toward eastern and northern exposures, a well developed growth can be observed of a large number of perennial plants, most of which are composites such as *Solidago rigida* L., *S. Drummondii* T. & G., *Aster turbinellus* Lindl., *A. patens* Ait., *Helianthus occidentalis* Riddell, *H. petiolaris* Nutt., *H. orgyalis* DC., *Lepachys pinnata* (Vent.) T. & G., *L. columnaris* (Sims) T. & G., *Ambrosia bidentata* Michx., *A. psilostachya* DC., *Silphium laciniatum* L., *Elephantopus carolinianus* Willd., *Vernonia crinita* Raf., *V. altissima* Nutt., *Rudbeckia triloba* L., and the very beautiful *Echinacea purpurea* DC. Species of other families which are often found here are *Monarda fistulosa* L., *M. mollis* L., *M. punctata* L., *M. citriodora* Cerv. (rare), *Pycnanthemum flexuosum* (Walt.) B.S.P., *P. pilosum* Nutt., *Scutellaria canescens* Nutt., *S. pilosa* Michx., *Pentstemon Cobaea* Nutt., *P. hirsutus* (L.) Willd., *Gerardia grandiflora* Benth. (often between oaks), *G. flava* L., *Linum virginianum* L., *Euphorbia corollata* L., *E. heterophylla* L. (rare in Butler County), *Apocynum androsaemifolium* L., *A. cannabinum* L., *Asclepias tuberosa* L. (rare), *A. purpurascens* L., *A. quadrifolia* Jacq., *A. verticillata* L. (occasionally), *Amsonia Tabernaemontana* Walt.; also *Gaura coccinea* Pursh, *Cuphea petiolata* (L.) Koehne, *Tephrosia virginiana* (L.) Pers., *Baptisia bracteata* (Muhl.) Ekl., and *Pteris aquilina* L. Several of these species are also to be found on treeless barrens, and some of them are common on the prairie-like areas. A semi-parasite growing on the roots of oaks, *Comandra umbellata* (L.) Nutt., is very common in the entire region.

All these perennial plants usually form a dense vegetation, where a struggle for maintenance seems to exist, although there do not appear to be large areas covered only by one or two species.

Where a little creek passes through the dry hills, although it may be dry during the greater part of the summer, different vegetation is always found to have established itself. The soil contains more organic matter, and on account of the humus it contains and keeps its moisture longer and better than the surrounding loam. In such areas one finds, besides the already mentioned spring flora, several other interesting species. *Oakesia sessiliflora* (L.) Wats. forms whole groups; the creeping *Asarum canadense* L. covers whole patches, also *Pedicularis canadensis* L., *Heuchera hirsuticaulis* (Wheelock) Rydb., and *Mitella diphylla* L.; whereas *Trillium recurvatum* Beck and the early flowering annual *Collinsia verna* Nutt. are always to be met with. These species are all to be seen flowering in the spring and until early in summer, but later in the season they are gradually followed by *Lobelia inflata* L., *Silene stellata* (L.) Ait. f., *Spigelia marilandica* L., *Tradescantia virginiana* L., *T. rosea* Vent., and a few species of ferns, also such species as we find in the ravines and little valleys.

The climbing plants are not as well represented as they are in the valleys or in the rich lowlands. Very conspicuous here are two species of *Passiflora*, namely *P. incarnata* L., with large flesh-colored flowers, and *P. lutea* L.,

with small pale to greenish-yellow flowers. The former species is commoner in the southern counties, whereas the latter is further distributed toward the north. They grow either around twigs and stems of shrubs and young trees or are to be found without any support on treeless areas. Also *Vitis rupestris* Scheele grows sometimes in similar places.

Descending the above-described types of barren hills, the plant growth becomes different, mainly for two reasons: (1) a higher water content of the soil; and (2) a larger percentage of organic matter in the soil, which has partly accumulated after heavy rains from higher parts of the hills.

Tree growth is here entirely different; oaks like *Quercus marilandica* have disappeared, and are replaced by *Q. alba* and *Q. rubra*; *Juglans nigra* L. is here commoner; and other new species come to the front, such as *Betula lenta* L., *B. nigra* L., *Carpinus caroliniana* Walt., *Ostrya virginiana* (Mill.) K. Koch. Where a little valley is reached through which a little stream flows the number of various species of trees becomes high; it can not be said that a certain species predominates, as they form a mixture of *Populus heterophylla* L., *P. deltoides* Marsh., *Alnus incana* (L.) Moench, *Salix nigra* Marsh., and *Platanus occidentalis* L. on very wet and fertile soil; whereas further back these are accompanied by *Celtis occidentalis* L., *C. mississippiensis* Bosc., *Morus rubra* L., *Gleditsia triacanthos* L., *Pyrus coronaria* Mill., *Ulmus racemosa* Thom., *Gymnocladus canadensis* Lam. *Cercis canadensis* L., *Crataegus* sp., *Prunus serotina* Ehrh., and *Maclura aurantiaca* Nutt. (especially common in the southern counties). Impenetrable thickets composed of many species of shrubs and young trees are here practically always present; they are frequently composed of whole groups of *Corylus americana* Walt., *Sambucus canadensis* L., *Hydrangea arborescens* L., *Rhamnus lanceolata* Pursh, *Itea virginica* L., and *Physocarpus opulifolius* (L.) Maxim. In the more southern counties, such as Butler and Ripley counties, one finds in similar localities species which belong to the southern part of the state, among which I mention in the first place *Neviusia alabamensis* Gray, which the writer found in a single individual about 12 kilometers west of Poplar Bluff growing in a southeastern exposure on a somewhat sandy-loam slope of a small hill near the bank of a little creek; previously this species has been found only in a few localities in the state of Alabama. *Decumaria barbara* L. has been found along the bank of a little stream (Davis Creek) in Carter County, in but three individuals. Along such creeks and little river valleys there are a great many different kinds of climbing plants, especially *Ampelopsis quinquefolia* L., *Cissus stans* Pers., *Vitis cinerea* Engelm., *V. riparia* Michx., *V. aestivalis* Michx., *Rhus Toxicodendron* L., *Tecoma radicans* (L.) Juss., and *Menispermum canadense* L. Along the lower parts of the slopes and near creek beds is *Gelsemium sempervirens* (L.) Ait. f., a little vine of the southern states which sometimes occurs in some parts of Butler and Ripley counties; on the other hand, I was never able to find it in the more northern counties

such as Iron and Madison. Of herbaceous and annual climbers, *Ipomoea pandurata* (L.) Mey., both Passifloras, *Sicyos angulatus* L., *Echinocystis lobata* (Michx.) T. & G., *Humulus Lupulus* L., and *Smilax herbacea* L. are common.

The spring flora is in such places well represented by various species of different families; besides the plants already mentioned from the forests of the hills (*Oxalis violacea* and *Hypoxis hirsuta* excepted), there are present along moist places *Cardamine bulbosa* (Schreb.) B.S.P., *Ranunculus septentrionalis* Poir., *R. fascicularis* Muhl., *Viola blanda* Willd., *Sanguinaria canadensis* L., *Peltandra virginica* (L.) Kunth, and *Dicentra Cucullaria* (L.) Bernh.; and *Mertensia virginica* (L.) Link not seldom occurs in large patches. Later, in the early summer, flower *Hydrastis canadensis* L., *Stylophorum diphyllum* (Michx.) Nutt. (rare), *Hybanthus concolor* (Forster) Spreng., *Dodecatheon Meadia* L., *Anemone virginiana* L., *A. pennsylvanica* L., and rarely *Cypripedium candidum* Muhl. and *Pogonia trianthophora* (Sw.) B.S.P. In the summer and autumn the ground is covered by a pure association of *Impatiens fulva* Nutt., with but a very few other species growing in between. Where *Impatiens* is absent there is usually found a diversified flora composed of *Cardamine pennsylvanica* Muhl., *Iris versicolor* L., *Laportea canadensis* (L.) Gaud., *Boehmeria cylindrica* (L.) Sw., *Arisaema triphyllum* (L.) Schott, and *A. Dracontium* (L.) Schott. Pteridophytes are well represented by *Adiantum pedatum* L., *Phegopteris hexagonoptera* (Michx.) Fee, *Asplenium acrostichoides* Sw., *Onoclea sensibilis* L., *Osmunda Claytoniana* L., *Botrychium virginianum* (L.) Sw., and sometimes *Ophioglossum vulgatum* L. In Butler County and other southern counties *Hymenocallis occidentalis* (Le Conte) Kunth, with its bright, beautiful white flowers, can frequently be observed along small river valleys.

During the latter part of the summer one finds, besides the nettle association of *Boehmeria* and *Laportea*, scattered almost everywhere, *Campanula americana* L., *Scrophularia marilandica* L., *Parietaria pennsylvanica* Muhl., *Circaea lutetiana* L., *Hydrophyllum canadense* L., *Muhlenbergia mexicana* (L.) Trin., *M. racemosa* (Michx.) B.S.P., *Uniola latifolia* Michx., *Diarrhena diandra* (Michx.) Wood, and several groups of *Eupatorium urticaefolium* Reich. and *Solidago latifolia* L.

In some of the counties the author has observed woods of *Pinus echinata* Mill. Once these were very common and extensive, but practically all have been cut down by lumber companies; only very little has been left. The writer found west of Carter County a small forest where this species of pine formed practically the entire growth under the trees. Here and there the small-shrub vegetation is composed of little thickets or single individuals of *Symphoricarpos orticulatus* Moench, *Ceanothus americanus* L., and in open places of the woods of a single *Rhus typhina* L., whereas very large areas are entirely shrubless. The general aspect of the areas covered with *Pinus echinata* is generally that of dry, stony lands.

Where limestone outcrops occur along considerable areas in the mountains, *Juniperus virginiana* L. usually covers large parts and forms pure stands. In Iron County these conifers sometimes are very common, growing toward the summits of the mountains and along the edges of the cliffs. Lower down, *Celtis occidentalis* L., *Acer Negundo* L., *Amelanchier canadensis* (L.) Medic., *Fraxinus quadrangulata* Michx., *Morus rubra* L., *Quercus marilandica* Muench., *Q. Muhlenbergii* Engelm., *Diospyros virginiana* L., *Carya alba* (L.) Koch, and, under these, the shrubs *Cornus asperifolia* Michx., *Viburnum rufidulum* Raf., and *Hydrangea arborescens* L. are always present. On treeless portions of such rock outcrops the plant growth is very much exposed to extreme heat and drought; therefore the flora is often xerophytic or semi-xerophytic, except near dripping ledges and little springs; here *Selaginella rupestris* (L.) Link, *Woodsia obtusa* (Spreng.) Torr., *Cystopteris fragilis* (L.) Bernh., *Aquilegia canadensis* L., *Solidago Drummondii* T. & G., and *Heuchera hispida* Pursh are predominating; in places less rich in soil *Pellaea atropurpurea* (L.) Link and *Cheilanthes Feei* Moore usually are the commonest species; on rock outcrops, somewhat shaded, in Ripley County, the writer found many plants of *Asplenium viride* Huds. and *Pellaea dealbata* Car. and a few individuals of the southwestern *Pellaea mucronata* DC.; on the highest elevations of such cliffs and bare mountain summits, *Draba cuneifolia* Nutt., *D. brachycarpa* Nutt., and *Androsace occidentalis* Pursh are prevalent. On flat places *Astragalus distortus* T. & G., and *Scutellaria parvula* Michx. are very common. Where the situation is shadowed by some tree or by rocks and is somewhat moist, but nevertheless stony and covered with very little soil, a dense association of *Camptosorus rhizophyllus* (L.) Link, the well-known walking fern, covers several rocks, growing from one stone to the other and in this way sometimes covering considerable areas. Between rocks, *Cystopteris bulbifera* (L.) Bernh., *Notholaena dealbata* (Pursh) Kunze, *Woodsia obtusa* (Spreng.) Torr., *Polystichum acrostichoides* (Michx.) Schott, *Asplenium platyneuron* (L.) Oakes, *A. Bradleyi* DC. Eaton (rare), *Erigeron philadelphicus* L., *Arabis dentata* T. & G., and *Opuntia Rafinesquii* Engelm. occur almost everywhere.

Where the rocky aspect gradually disappears and more soil accumulation is to be seen, such species occur as *Desmanthus illinoensis* (Michx.) MacM., *Schrankia uncinata* Willd., *Cassia Medsgeri* Shafer, *C. nictitans* L., *Agave virginica* L., *Cooperia Drummondii* Herb., *Eryngium yuccifolium* Michx., *Verbascum Thapsus* L., *Desmodium paniculatum* (L.) DC., *D. marilandicum* (L.) DC., *Psoralea tenuiflora* Pursh, and practically all composites which are to be found in the above-described hills of the oak facies.

The prairie flora is not here well represented; although sometimes barren, treeless areas appear several square kilometers in extent. They occur in almost any of the counties in the Ozarks as far as they were studied. The principal vegetation is composed of grasses, especially *Agropyron spicatum* Scribn., *Bouteloua oligostachya* (Nutt.) Torr., *B. curtipendula*

(Michx.) Torr., and *Panicum* sp.; further, *Liatris squarrosa* Willd., *L. scariosa* Willd., *Petalostemum purpureum* (Vent.) Rydb., *Euphorbia corollata* L., *Croton monanthogynus* Michx., *Astragalus mexicanus* A. DC., and especially *Trifolium stoloniferum* Muhl. and *Plantago aristata* Michx. predominate; like the true prairies, these barren places have no vernal flora.

This description of the plant societies and associations of the Ozark uplift of the southeastern portion of Missouri gives a general idea of the nature of its flora.

The lowlands, covering about 7,500 square kilometers and lying about 300 feet above sea level, are largely composed of residue from the Mississippi River and its tributaries, such as the Black River, St. Francois River, and others. These bottom lands are composed of various types of very fertile loam soils. They are complex in origin, as the various rivers obtained their material from such sources as the residual uplands, the plains, the loessial and glacial prairies; consequently they differ from one another in composition and color, ranging from sandy loam to silty loam. The soils west of Crowley's Ridge, representing the old valley of the Mississippi River, are very old; usually they are grey in color; through poor drainage and constant leaching a considerable loss of lime, iron, and sometimes of phosphorus has resulted. A silty loam of a great depth is the principal soil of this region; it includes most of the land between the upland and the western part of Crowley's Ridge. The northern part, however, consists of recent alluvium, derived from the uplands, and contains at various places much organic matter. The subsoil usually is a drab silty clay.

West of Crowley's Ridge, in Stoddard County and Ripley County, a relatively large area is found with fine sandy loam; it is greyish brown to yellowish grey, whereas the subsoil is composed of sandy clay; it contains many iron concretions, which may result in hardpan formation. This country stands three to eight decimeters above the surrounding lowlands.

From about Cape Girardeau County throughout the lowlands toward the boundaries of Arkansas, the soil is heavy and contains much organic matter, whereas the subsoil is of a close structure. These areas are the lowest of any part of southeastern Missouri, which fact has resulted in the formation of swamps of considerable extent.

These swamps are of extreme interest to the ecologist; many formations and associations are here to be encountered, starting in the floating plant associations of Lemnas and ending in the strange swamps with *Taxodium* and monotonous *Nyssa* forests.

Following the various facies of the different plant associations, one may readily distinguish the stagnant pools and ponds, the surface of the water thickly covered by floating plants most of which belong to the Lemnaceae; a pond is covered either by a single species or by several. The following are found: *Wolffia punctata* Griseb., *W. papulifera* C. H. Thomps. (rare), *Wolffiella floridana* (J. D. Sm.) Thomps., *Spirodela polyrrhyza* (L.) Schleid., *Lemna valdiviana* Phil., *L. perpusilla* Torr., and *L. minor* L. *Azolla caro-*

liniana Willd. is also very common in quiet or almost stagnant waters, so covering the surface of the water as to give the appearance of a large lawn. *Riccia natans* L. is frequently to be found but is never as common as the other species belonging to the floating flora. These species are, apart from several algae, the first appearance of any vegetation in these watery areas.

About seven meters below the water surface there are a few species of plants rooting in the mud; a very few individuals may here be found of *Isoetes Engelmanni* A. Br.; between the depths of five and seven meters a number of submerged species are prevalent. Where the water is clear, large areas can be noticed of "meadows" with *Elodea canadensis* Michx.; where this growth is not as dense, *Potamogeton Hillii* Morong, *P. pusillus* L., and *Najas flexilis* (Willd.) Rostk. & Schmidt are present; and occasionally *Ceratophyllum demersum* L. and some *Vallisneria spiralis* L. In a few ponds I found whole areas filled with *Myriophyllum heterophyllum* Michx., and nothing else. In slowly flowing streams and little rivers, *Batrachium aquatilis* L., and especially *Heteranthera graminea* Vahl, are very common; the Black River is for several miles covered with the latter species.

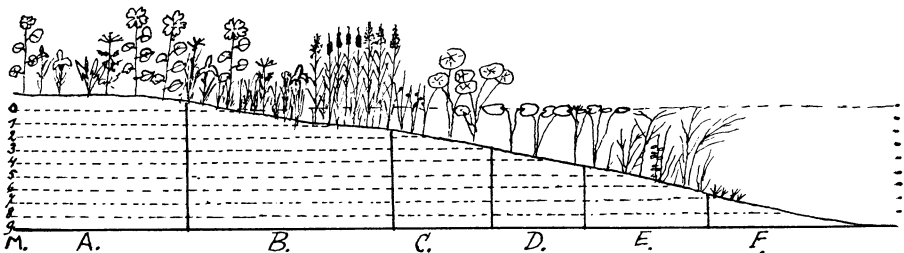


FIG. 1. A swamp formation. A, Hibiscus, Sium, Cicuta, Rumex, Iris, Sagittaria, Mimulus, Lobelia. B, the same, and Phragmites, Typha, Acorus, Sparganium. C, Scirpus, Nelumbium. D, Nymphaea, Nuphar. E, *Potamogeton Hillii*, *Najas*, *Elodea*, *Ceratophyllum*, *Isoetes*. F, *Isoetes*.

The facies of the water lilies and their associates are formed at a depth of from two to four meters below the surface; these *aquatilis natantes* form dense masses of *Nymphaea odorata* Ait. and *Nuphar advena* Ait. Commonly found in these places are *Potamogeton hybridus* Michx., *P. americanus* C. & S., and *P. natans* L.; where the growth of water lilies is too dense the Potamogetons are unable to grow. Frequently they form pure associations without any other water plant. Between these are often found the above-described submerged species; whereas *Isoetes Engelmanni* becomes more frequent, *I. melanopoda* J. Gay is also noticed.

Toward the border of the lake the water-lily association includes considerable tracts of *Nelumbo lutea* (Willd.) Pers. often reaching the border of the lake and large pools. They may be considered as forming an in-

intermediate between the floating water plants and the amphibious vegetation; they root in the mud from $1\frac{1}{2}$ to 3 meters below the surface of the water. Here also several forerunners are growing of *Pontederia cordata* L. Taking these pure aquatic plants as a whole, there are relatively few species in comparison with the amphibious and semi-amphibious species along the edges of the lakes.

The margins of the ponds and lakes are surrounded by a great number of different species of amphibious plants; sometimes they form pure associations, but mostly they occur in societies of different species. From a depth of $\frac{1}{2}$ to 1 meter the lakes are thickly covered with *Scirpus lacustris* L., *S. fluviatilis* (Torr.) Gray (rare), *Typha latifolia* L., *Phragmites communis* L., *Sagittaria lancifolia* L., *S. graminea* Michx., *Acorus Calamus* L., *Zizania palustris* L., *Glyceria fluitans* (L.) R. Br. (also sometimes between the water lilies), *G. nervata* (Willd.) Trin., *Dulichium arundinaceum* (L.) Britton (rare), *Iris fulva* Ker, and *I. hexagona* Walt. In less pure associations are to be seen *Alisma Plantago* L., *Sparganium eurycarpum* Engelm., *S. lucidum* Fern. & Eames; *Nelumbo lutea* also often grows here, although in few individuals. A very interesting species growing in ponds, borders of lakes, and even on mud flats, is *Thalia dealbata* Roscoe, a member of the Marantaceae which reaches here in this region one of its northern limits. Frequently it is associated with the beautiful flowering *Hymenocallis occidentalis* (Le Conte) Kunth. Mud flats and shallow ponds are for several miles covered with *Polygonum Muhlenbergii* (Meisn.) Wats., hardly showing any other species in their association; their rootstocks are very deeply imbedded in the mud. Also *Cicuta maculata* L., *Saururus cernuus* L., and *Jussiaea diffusa* Forst. are growing amongst such mud plants. When the mud flats become partly dry in summer there may be for a time a vegetation of any species whose seeds happen to drop and to germinate there, but these always disappear when the land becomes inundated again. To such species belong *Polygonum Hydropiper* L., *Solanum carolinense* L., *Humulus alatus* Ait., *Lippia lanceolata* Michx., *Rotala ramosior* (L.) Koehne, and a few others. When such mud flats happen to remain dry, these and other species cover the surface entirely; then a struggle for life soon eradicates some of the least resistant individuals, and eventually entire species.

Other amphibious plants along the margins of lakes are *Equisetum hyemale* L., *Cicuta maculata* L., *Sium cicutaefolium* Schrank, *Rumex crispus* L., *R. verticillatus* L., *Jussiaea diffusa* Forst., *Bacopa rotundifolia* (Michx.) Wettst., *Senecio aureus* L., *Carex monile* Tuckerm., *C. conjuncta* Boott, *Mimulus ringens* L., *Stachys palustris* L., *Diodia virginiana* L., *Ranunculus abortivus* L., *Ludvigia palustris* (L.) Ell., *Lobelia siphilitica* L., *L. cardinalis* L., *Nasturtium palustre* L., and (in large tracts) *Hibiscus lasiocarpus* Cav.

Very large areas of swamps are covered with *Taxodium distichum* (L.) Richard and *Nyssa aquatica* L. Gigantic trees of the former as well of the latter form pure stands or grow mixed near one another covering several square kilometers in extent. The *Taxodium* forest has only few associates

especially in deep swamps; they grow successfully only when moisture is abundant. *Taxodium* is "the" tree for alluvial swamps. Lands which are overflowed regularly by rivers are especially suitable for this species; only in the dry seasons do a part of these forested mud fields become dry. The trees develop a straight stem; where water is deep, the base of these stems is always broad and more or less ridged; where water is more or less shallow, or in localities not as much subject to heavy overflow, this base is not as broad or ridged and is normally developed like that of ordinary trees. A peculiar characteristic of these trees consists of the development of knees,

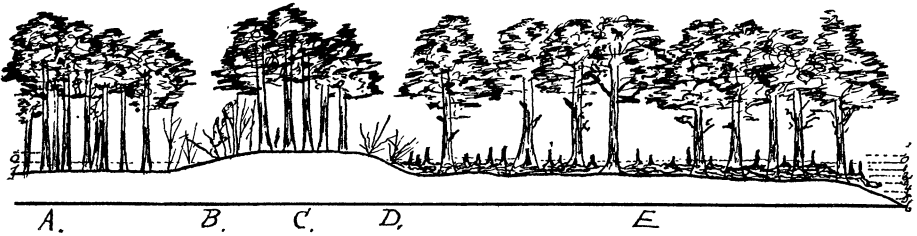


FIG. 2. A swamp forest. A, *Nyssa sylvatica*. B, *Salix nigra*. C, *Acer rubrum*, *Quercus alba*, *Q. rubra*, *Platanus occidentalis*, etc. D, *Cephalanthus occidentalis*. E, *Taxodium distichum*.

vertical outgrowths of the superficial root system, which give a strange aspect to the physiognomy of this plant association. Knees occur only where the ground is covered for a long time or all the year round by water. These knees attain a height of from 4 to 15 decimeters; very occasionally they are higher. According to various authors they serve the purpose of supplying oxygen to the root system in the mud, as well as strengthening the support of the tree on the surface.

Another representative of the swamps which is frequently associated with *Taxodium* is *Nyssa aquatica* L. A pure forest tree of medium age shows a peculiar aspect on account of the straight, smooth stems; hundreds of such trees have the appearance of as many straight pillars. Old individuals attain a height of from 18 to 28 meters. The base of old stems is thickly covered by mosses and by a small fern, *Polypodium polypodioides* (L.) Hitchc. Where *Taxodium* swamps are not too deep there exists an immense undergrowth of *Polygonum Muhlenbergii* (Meisn.) Wats. On outstanding mud flats or in open shallow places of the *Taxodium* forest, *Cephalanthus occidentalis* L. is of common occurrence, forming dense thickets. Sometimes a single *Salix nigra* Marsh., or rarely *Dirca palustris* L., occurs; in some swamps the author observed a dense growth of *Leitneria floridana* Chapm. in places similar to those occupied by *Cephalanthus*, while on logs *Itea virginica* L. often occurs.

Where the swamp becomes shallow, or where it is even dry during a large part of the season, a greater variation in species of trees and shrubs at

once manifests itself. *Taxodium* and *Nyssa* become scarcer, and a mixed stand appears of *Acer rubrum* var. *Drummondii* (H. & A.) T. & G., *Planera aquatica* (Walt.) J. F. Gmel., *Populus deltoides* Marsh., *P. heterophylla* L., *Carya aquatica* (Michx. f.) Nutt., *Fraxinus profunda* Bush., *Styrax americana* Lam., and *Gleditsia aquatica* Marsh.; the latter sometimes forms pure, impenetrable stands. Frequently there occur here treeless areas which are usually covered with *Juncus acuminatus* Michx., *J. scirpoides* Lam., *Eleocharis acuminata* (Muhl.) Nees, *E. intermedia* (Muhl.) Schultes, *E. palustris* (L.) R. & S., *Cyperus flavescens* L., and *C. acuminatus* Torr. & Hook., besides most species which are also to be found along the treeless margins of the lake. In some old mud ponds where a part of the year water has been left, characteristic groups of *Salix nigra* Marsh. and *S. longifolia* Muhl. cover large stretches.

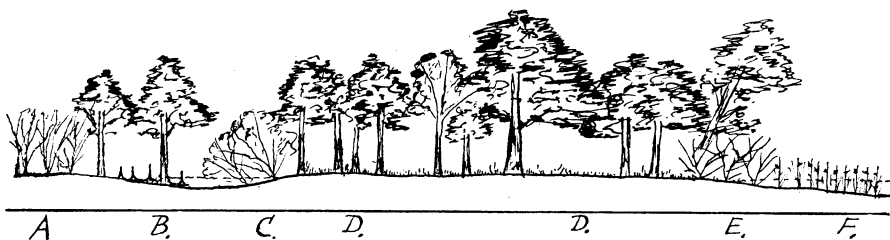


FIG. 3. A mixed forest. A, *Leitneria floridana*. B, *Taxodium distichum*. C, *Salix nigra*. D, mixed growth of *Platanus occidentalis*, *Morus rubra*, *Celtis occidentalis*, *Quercus* sp., *Ulmus americana*, etc. E, *Cephalanthus occidentalis*, *Sambucus canadensis*. F, swamp with *Scirpus lacustris*.

On the higher elevations of the bottom lands which are not as often subject to overflow, with the exception of high floods caused by such streams as the Black River and the St. Francois River, dense forests are to be found of a very diversified tree growth. On account of the richness of the soil the trees attain considerable height and thickness, one of the largest being *Platanus occidentalis* L., which is followed in size by beautiful individuals of *Quercus alba* L., *Q. rubra* L., *Q. macrocarpa* Michx., *Q. bicolor* Willd., *Q. Michauxii* Nutt., *Ulmus fulva* Michx., *U. americana* L., *Tilia americana* L., *Juglans nigra* L., *J. cinerea* L., *Sassafras officinale* Nees & Eberm., as well as of *Quercus phellos* L., *Morus rubra* L., *Celtis occidentalis* L., *C. mississippiensis* Bosc., *Liquidambar styraciflua* L., *Acer rubrum* (H. & A.) T. & G., *Fraxinus americana* L., *Carya alba* (L.) Koch, *C. illinoensis* (Wang.) K. Koch, *Pyrus coronaria* L., *Aesculus pavia* L., *Gymnocladus canadensis* Lam., *Cercis canadensis* L., *Magnolia tripetala* L., *Liriodendron tulipifera* L., *Cladrastis lutea* (Michx. f.) Koch, *Crataegus* sp., *Populus heterophylla* Marsh., and *P. deltoides* Marsh. All these species grow near one another, not one forming a pure stand with the exception of *Asimina triloba* Dunal, which often covers whole thickets several acres in extent. On such lands *Taxodium* and *Nyssa* are very rare.

The author has endeavored to give in tabular form (table 3) the number of trees of certain species of a few areas in these bottom lands, also the diameter of the thickest trees he found in this region.

TABLE 3

Name of Tree	A Forest in Dunklin County %	A Forest in Butler County %	A Forest in Butler County %	A Forest in St. Francois County %	Diameter of Thickest Tree Observed (dm.)
<i>Taxodium distichum</i> (L.) Rich.	100	—	76	2	31
<i>Nyssa aquatica</i> L.	—	100	24	1	15
<i>Acer rubrum</i> var. <i>Drummondii</i> (H. & A.) T. & G.	—	—	—	8	8
<i>Platanus occidentalis</i> L.	—	—	—	6	22
<i>Quercus alba</i> L.	—	—	—	11	12.5
<i>Q. rubra</i> L.	—	—	—	4	11
<i>Q. phellos</i> L.	—	—	—	2	5
<i>Q. Michauxii</i> Nutt.	—	—	—	1.5	15
<i>Juglans nigra</i> L.	—	—	—	2	12
<i>J. cinerea</i> L.	—	—	—	1	8
<i>Carya alba</i> (L.) Koch.	—	—	—	4	7
<i>C. illinoensis</i> (Waug.) K. Koch.	—	—	—	1	9
<i>Morus rubra</i> L.	—	—	—	2.5	6
<i>Tilia americana</i> L.	—	—	—	0.5	8
<i>Liriodendron Tulipifera</i> L.	—	—	—	0.5	14
<i>Fraxinus americana</i> L.	—	—	—	2	11
<i>Celtis occidentalis</i> L.	—	—	—	3	4
<i>Ulmus americana</i> L.	—	—	—	2.5	22
<i>Salix nigra</i> Marsh.	—	—	—	20	9
<i>Liquidambar styraciflua</i> L.	—	—	—	5	12
<i>Planera aquatica</i> (Walt.) J. F. Gmel.	—	—	—	2	2
<i>Populus heterophylla</i> L.	—	—	—	3	8
<i>Leitneria floridana</i> Chapm.	—	—	—	5	0.4
<i>Gymnocladus canadensis</i> Lam.	—	—	—	0.5	4
<i>Asimina triloba</i> Dunal.	—	—	—	10	2.5

The *Vitis* association is very pronounced in such moist forests and along river banks. Dense and dark entanglements through which it is difficult to penetrate are formed by *Vitis cordifolia* Michx., *V. riparia* Michx., *V. cinerea* Engelm., *Ampelopsis quinquefolia* Michx., and *A. cordata* Michx.; to this list may be added *Menispermum canadense* L., *Cocculus carolinus* (L.) DC., *Celastrus scandens* L., *Rhus Toxicodendron* L., *Tecoma radicans* (L.) Juss., *Bignonia capreolata* L., *Aristolochia macrophylla* Lam., *Lonicera dioica* L., *Wisteria macrostachya* Nutt., and *Clematis virginiana* L. Some of these reach the summits of the high trees, and attract much attention during the flowering period. Herbaceous climbers are here represented by *Smilax herbacea* L., *S. rotundifolia* L., *S. Bona-nox* L., *Dioscorea villosa* L., *Passiflora incarnata* L., and *Sicyos angulatus* L.

Where forest trees make up a dense formation there are but few species of shrubs; but along the edges of these woods and where trees are more scattered there are several species of shrubs and small trees, the principal ones which are found being *Carpinus caroliniana* Walt., *Ostrya virginiana*

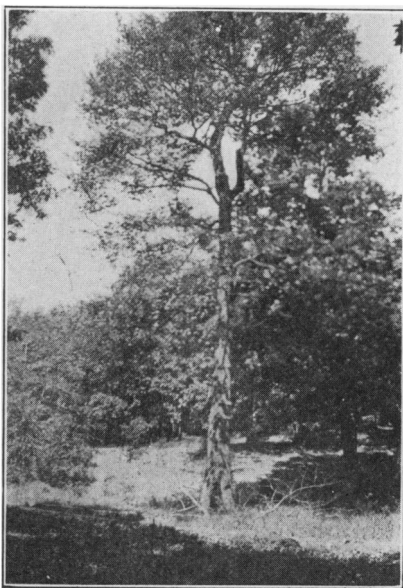
(Mill.) K. Koch, *Ptelea trifoliata* L., *Ilex decidua* Walt., *I. opaca* Ait., *I. Cassine* L., *Cephalanthus occidentalis* L., *Staphylea trifolia* L., *Xanthoxylum americanum* Mill., *X. Clava-Herculis* L. (rare), *Sambucus canadensis* L., *Corylus americana* Walt., and *C. rostrata* Ait. (both forming dense thickets), *Cornus stolonifera* Michx., *C. florida* L., *Hamamelis virginiana* L., *Adelia acuminata* Michx., *Styrax americana* L., *Lindera Benzoin* Blume, *Physocarpus opulifolius* (L.) Maxim., *Ribes gracile* Michx., *Rosa carolina* L., *Amorpha fruticosa* L., *Cercis canadensis* L., *Chionanthus virginica* L., *Viburnum prunifolium* L., and *Amelanchier canadensis* (L.) Medic.

In the spring and early summer the woods are extremely attractive during the flowering period of such plants as *Magnolia*, *Cercis*, *Chionanthus*, *Adelia*, *Cornus*, and *Asimina*.

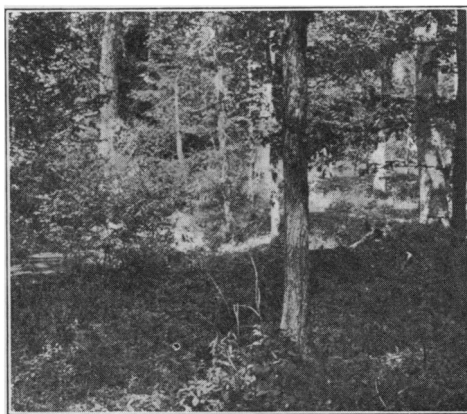
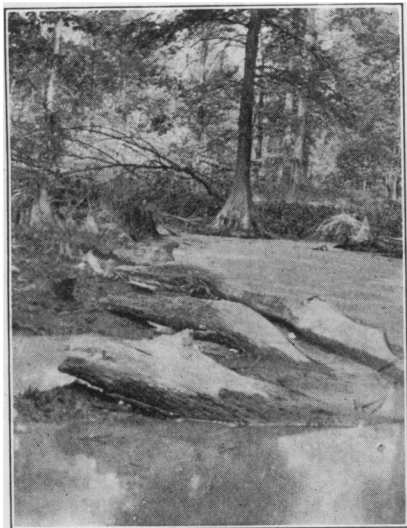
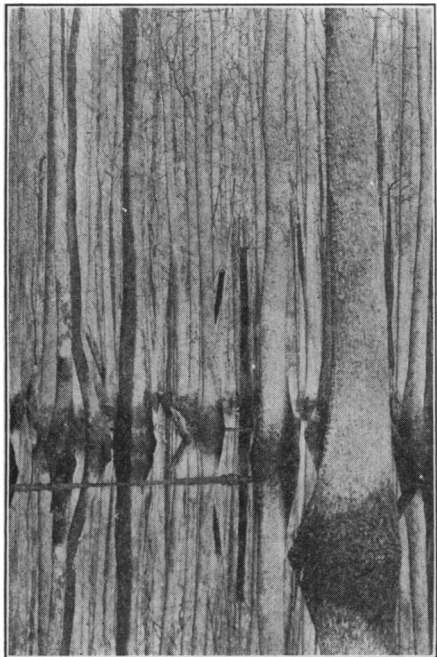
During the spring several perennial plants flower. One of the earliest is *Symplocarpus foetidus* (L.) Nutt., of which the spadix at first appears and later in summer the broad, veiny leaves. *Phlox divaricata* L. shows its bright blue flowers in almost any part of the woods. *Mertensia virginica* (L.) Link frequently covers large patches between the trees. Other vernal plants which are of common occurrence are *Claytonia virginica* L., *Uvularia grandiflora* Sm. (rare), *Erythronium americanum* Ker, *E. albidum* Nutt., *Trillium recurvatum* Beck, *T. grandiflorum* (Michx.) Salisb. (rare), *Dodecatheon Meadia* L., *Trientalis americana* (Pers.) Pursh, *Podophyllum peltatum* L., *Thalictrum purpurascens* L., *Viola blanda* Willd., *Arisaema triphyllum* L., and *Hydrastis canadensis* L.

During summer one finds in these dense forests extensive areas covered with *Boehmeria cylindrica* (L.) Sw., *Pilea pumila* (L.) Gray, and *Laportea canadensis* (L.) Gaud., forming the nettle association. In less dense areas there is a diversified perennial vegetation of *Rudbeckia laciniata* L., *Eupatorium coelestinum* L., *E. urticaefolium* Reich., *E. perfoliatum* L., *Elephantopus carolinianus* Willd., and clumps of the beautiful flowering *Spigelia marilandica* L.; the bright scarlet flowers of *Lobelia cardinalis* L. are visible at a long distance. Between the various herbs creeps *Eryngium prostratum* Nutt., while at some places *Commelina virginica* L. is very common. Tracts of land which are denuded of trees are covered with *Actinomeris squarrosa* Nutt. Of other common species I will mention *Silphium perfoliatum* L., *Ambrosia trifida* L., *Lactuca ludoviciana* (Nutt.) Riddell, *Botrychium virginianum* (L.) Sw., *B. ternatum* (Thunb.) Sw. and *Adiantum pedatum* L.

The bottom lands along the Mississippi in the southeastern section of the state are to a large extent covered by big woods of the same type, mixture, and character as those described above in the swamps and somewhat higher lands; marshes are here common. Directly along the shores are dense stands of *Phragmites communis* L., *Cyperus acuminatus* Torr. & Hook., and *Fimbristylis autumnalis* (L.) R. & S. Here and there some individuals of *Thalia dealbata* Roscoe and *Pontederia cordata* L. may be noticed, whereas other parts of the shores are practically bare. Mud flats



UPHOF: PLANTS IN SOUTHEASTERN MISSOURI



UPHOF: PLANTS IN SOUTHEASTERN MISSOURI

along the river during the rainless periods have the same type of vegetation as the mud flats of the lowlands described elsewhere.

The margins of the islands in the Mississippi are also covered by the vegetation above described. On older islands thickets of *Salix nigra* and *Adelia acuminata* are very predominant. *Populus deltoides*, *P. heterophylla*, *Prunus serotina*, and *Betula nigra* are also generally met with. On the largest islands *Taxodium distichum*, *Nyssa sylvatica*, and such trees and shrubs as belong to the true swamp forests often appear.

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EXPLANATION OF PLATES

PLATE I

Upper left: *Hymenocallis occidentalis* in lowlands; Dunklin County.

Upper right: *Monarda Bradburiana* under young oaks; in hills, western Butler County.

Lower left: *Echinacea purpurea* among several other species of perennial plants; near the edge of a forest, Iron County.

Lower right: Hills covered with *Quercus marilandica*; in front, a specimen of *Nyssa sylvatica*, Butler County.

PLATE II

Upper left: A pure stand of *Nyssa sylvatica*; Butler County.

Upper right: *Pinus echinata*; Carter County.

Lower left: *Taxodium distichum* formation; a mixed forest in the background; eastern Butler County.

Lower right: Mixed forest growth along a stream at the base of a hill; undergrowth largely composed of *Impatiens fulva*; Ripley County.